The interactive effects of disturbance and nutrient enrichment on species diversity and biomass of intertidal rocky-shore communities

by
Maya C. Pfaff

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Zoology Department
University of Cape Town, South Africa

Supervisor
Prof. G.M. Branch

This study is dedicated to Little Maya Mälzer

and the hope I place in the next generation to care for our planet

DECLARATION

This thesis documents original research carried out as student of the Zoology Department, University of Cape Town from 2003 to 2004. The presented work is my own, except where otherwise stated in the text.

Signed by candidate

Maya Pfaff

05-05-05

Date

ACKNOWLEDGEMENTS

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GLOSSARY

Community structure: The composition of species in an assemblage, including their presence and relative abundances.

Disturbance: A mechanism that causes the reduction of biomass. Different attributes of disturbance include its type, intensity, frequency, extent, duration, predictability and scale.

Diversity: A range of hierarchical scales and indices have been applied to describe diversity. In this study diversity is expressed through species richness and evenness.

Evenness: A measure of the relative contribution of common and rare species in a species assemblage. Pielou's evenness index $J' = \Sigma[ln(p_i) * p_i] / ln(k)$, where p_i is the proportion of cover of species i relative to the total species cover, and k is species richness.

Productivity: The rate of production of organic matter by a community.

Species richness: The number of species per sampling unit.

Stress: Mechanisms that restrict growth or reproduction.

ABSTRACT

Unimodal patterns of diversity along gradients of both disturbance and productivity rank amongst the most celebrated generalizations in ecology, known as the *Intermediate Disturbance Hypothesis* (IDH) and *Productivity-Diversity Hypothesis*. However, doubt about their generality has arisen from studies that have failed to confirm the predicted patterns. Models suggest the interactive effects of disturbance and productivity on diversity to be responsible for the variability of diversity patterns. I conducted a 2-factorial field experiment (7 disturbance frequencies, 3 nutrient levels) on a sub-tropical intertidal rocky shore to test the dependence of the IDH on productivity (i.e. nutrient level). Treatment responses varied between three distinct community types found at the two study sites. At one site, the turf-dominated communities showed no effect of disturbance on species richness, evenness, dry mass, biotic cover or community composition. Nutrient additions statistically decreased evenness, yielded trends of increased dry mass and biotic cover, and affected community structure. At the other site, where encrusting algae dominated, disturbance increased evenness and decreased biotic cover. Nutrient enrichment produced increased species richness and dry mass, a trend of increased evenness, and changed community structure. Under high enrichment, a third type of community of mixed turf-forming and encrusting algae was formed and disturbance and productivity interacted to produce the decreasing portion of the IDH curve. Background disturbances exerted by sand, waves and intertidal stress may

have interfered with the disturbance treatment. Different mechanisms controlled species coexistence in different community types, some failing to fulfill all assumptions of the IDH. Generalizations about factors that affect diversity should therefore be based on mechanisms rather than patterns.

INTRODUCTION

How ecosystems respond to environmental fluctuations remains amongst the most fundamental questions in ecology. Do oscillations of the environment promote extinctions (Pimm 1991), or do they weaken inter-specific competition and thus promote species coexistence (Hutchinson 1961)? Beyond its purely scientific appeal, the issue has become vital in the context of current accelerated changes of the biosphere. Climatic shifts, habitat destruction and modification, pollution and introduction of invasive species are amongst the chief causes of a global decline of biodiversity (Soulé 1991; Pimm et al. 1995). The need to manage nature's responses to our doings urges ecologists to understand how the interplay of various environmental factors affects biodiversity and ecosystem functioning. With my research, I specifically attempt to tackle the interactive roles of two of the most prominent factors that influence species diversity: disturbance and productivity.

The role of disturbance

Hypotheses about the role of disturbance in community organisation form a cornerstone of ecological theory (Cooper 1926; Watt 1947; Hutchinson 1953, 1961; Paine 1966; Dayton 1971; Grime 1973, 1977; Menge 1976; Sousa 1979a, 1979b, 1984; Paine and Levin 1981; Airoldi 1998; Menge and Branch 2001).

In the past, coexistence of species was predominantly explained by equilibrium models. These focused on the properties of systems at an equilibrium point, at which communities reach relative stability in the course

of competition-driven succession, and to which they return after perturbation (Connell 1978). The maintenance of diversity is explained by factors that reduce competition and so prevent the exclusion of species, such as resource partitioning or predation. However, equilibrium concepts do not account for the transient patterns of diversity observed in nature, where environmental fluctuations (including disturbance) seem the norm and equilibrium conditions are rare or delusive (Hutchinson 1961; Connell 1978; Huston 1979). This led to a paradigm shift towards non-equilibrium models (Wu and Loucks 1995) focussing on the spatial and temporal dynamics of diversity and the significance of processes such as disturbance that promote the coexistence of species without the attainment of any fixed equilibrium point (Chesson and Case 1986).

One of the most frequently employed non-equilibrium models for species coexistence is the *Intermediate Disturbance Hypothesis,* hereafter IDH (Grime 1973; Horn 1975; Connell 1978; Sousa 1979a; Wilson 1990). The IDH proposes a unimodal (hump-shaped) pattern of diversity along a disturbance gradient (Fig.1).

The IDH is based on a trade-off between the competitive abilities of species and their colonization rates (Collins and Glenn 1997; Mackey and Currie 2001; Roxburgh et al. 2004; Shea et al. 2004). In absence of disturbance a small number of superior competitors (but poor colonizers) are thought to out-compete other resource users, and thus diversity is expected to be low. At the other extreme, frequent disturbances select for few opportunistic

Mechanism explaining low diversity in low disturbance regime	Mechanism explaining peak diversity at intermediate disturbance levels	Mechanism explaining low diversity in high disturbance regime	Disturbance – Diversity Theory
Dominance of few species that are superiour competitors	Coexistence of diverse species in patches of different successional age	Dominance of few species that are tolerant to disturbance or quick colonizers	***Intermediate Disturbance Hypothesis (IDH)*** (Connell 1978) ***Successional Mosaic Hypothesis*** (Chesson & Huntley 1997) ***Between Patch Mechanics*** (Wilson 1994)
Fast-growing populations out-compete poor competitors for nutrients (growth rate depends on productivity)	Trade-off between mortality by competitive displacement and disturbance favours coexistence of speceis	Population reduction and extinctions of less adapted species by frequent disturbance	***Dynamic Equilibrium Model*** (Huston 1979, 1994)

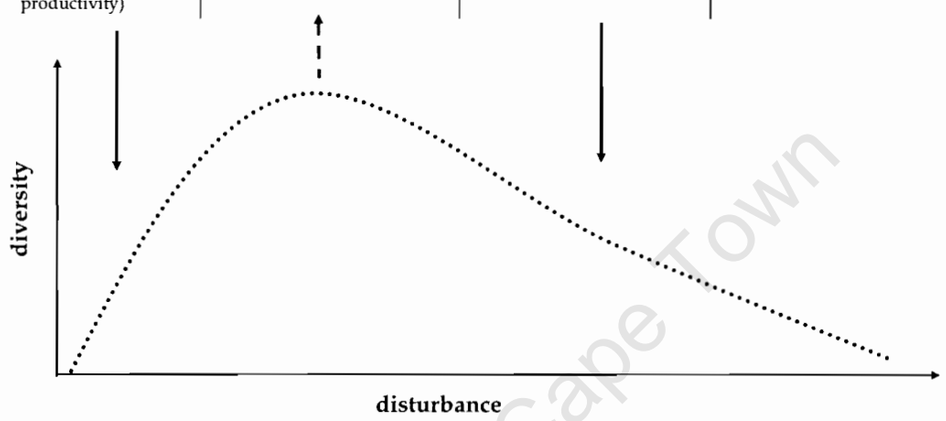

Figure 1: The unimodal relationship between disturbance and diversity explained by a variety of mechanisms. A disturbance gradient entails changes in frequency, extent, intensity, duration of disturbance or time since the last disturbance event. Two hypotheses are captured that explain the decline of species diversity in low and high disturbance regimes and why peak diversity occurs at intermediate levels of disturbance. The most prominent is the *Intermediate Disturbance Hypothesis (IDH*, also known as the *Successional Mosaic Hypothesis* or *Between Patch Dynamics)*. Note that the *Dynamic Equilibrium Model* incorporates productivity as an additional factor influencing the relationship.

colonizers (but inferior competitors), and diversity is also low. Maximum diversity is expected to occur at intermediate levels of disturbance, where strong competitors and opportunistic colonizers coexist in patches of different successional age and most species are granted a share of the limiting resources. Alternative names for the IDH that more specifically describe this mechanism have been suggested, such as the *Successional Mosaic Hypothesis* (Chesson and Huntly 1997) or *Between-Patch Mechanics* (Wilson 1994).

The attractiveness of the IDH as an explanation for patterns of diversity is expressed in a myriad of theoretical, experimental and observational studies (Wilson 1990; Mackey and Currie 2001). The proposed hump-shaped pattern has been explored in a wide range of habitats in terrestrial to aquatic systems and at different spatial scales spanning microcosms to landscapes (Shea et al. 2004).

Despite its fame, there remains intense dispute about the theoretical foundations of the IDH, its generality and its practicality. The following points of criticism have been raised:

1) The IDH seems appealingly elegant but is in fact too simplistic to account for changes in community structure (McGuinness 1987; Sheil and Burslem 2003).
2) There are fundamental difficulties in quantifying disturbance. Even when it is possible to measure the external forces that affect a system, it is often difficult to relate them to the extent of the actual impact on the community in question (Reynolds et al. 1993). Therefore, natural

disturbances are often compared by indirect measurements that lack biological meaning, such as "canopy height" in tree communities (Sheil and Burslem 2003) or "mixing depths" in plankton assemblages (Flöder and Sommer 1999). The generality of predictions about changes in diversity is thus limited to specific systems.

3) Related to the difficulty of quantifying disturbance is a commonly encountered circular argument around the definition of "intermediate levels" of disturbance, which is often arbitrarily assigned to the peak of diversity (Shea et al. 2004).
4) The IDH has been criticised for being non-falsifiable (Juhász-Nagy 1993; Huxham et al. 2000). Since it is difficult to test the purely qualitative predictions regarding changes in diversity along some disturbance gradient, the IDH cannot be perceived as a hypothesis *per se*, but rather as general conceptual framework based on certain assumptions about species interactions (Collins and Glenn 1997).
5) The IDH depends on a trade-off between competitive ability and colonisation potential of species that does not necessarily apply to natural systems (McGuinness 1987).
6) It has been claimed that the principals of the IDH apply to only the basal species in a food web, and that predictions about the diversity-disturbance relationship in multi-trophic assemblages must be made with caution (Wootton 1998).

7) A heated debate concerns the applicability of the IDH to scenarios where disturbance acts "within-" versus "between-patches" (Wilson 1990, 1994; Padisák 1994; Collins and Glenn 1997). "Within-patch" refers to uniform disturbance events affecting the whole system, whereas "between-patch" describes localized patchy disturbances. Originally, the mechanisms of the IDH were discussed in the context of sessile communities, where peak diversity was explained by the coexistence of patches of different successional age (Hutchinson 1953; Connell 1978), which corresponds to the "between-patch" scenario. The controversy arose from the experimental support of the IDH in planktonic communities (Padisák et al. 1993; Sommer et al. 1993), despite the argument that there should be no clear spatial patches in such homogeneously spread communities. Thus disturbances (perturbation) act "within-patch" affecting the whole community. Here the concept of disturbance frequency is replaced by the time interval since the last disturbance event and heterogeneity is perceived as being temporal rather than spatial. The application of the IDH to such "within-patch" settings was however strongly criticised as a misinterpretation of its underlying mechanisms (Wilson 1994). However, other authors have suggested that both "within-" and "between-patch" events can be assessed under the conceptual umbrella of the IDH, as long as it is recognized that separate mechanisms underlie the observed patterns (Chesson and Huntly 1997; Collins and

Glenn 1997; Sheil and Burslem 2003; Roxburgh et al. 2004). Experimental studies have confirmed the versatile applicability of the IDH for both "within-patch" (Flöder and Sommer 1999; Buckling et al. 2000) and "between-patch" scenarios (McCabe and Gotelli 2000).

8) Various authors have argued from a theoretical point of view that the hump-shaped pattern of the disturbance-diversity relationship may co-depend on other factors (Huston 1979, 1994; Chesson and Huntly 1997; Wootton 1998; Mackey and Currie 2000). This is most convincingly supported by a bulk of empirical studies that found the disturbance-diversity relationship to be neither consistently strong nor generally unimodal (Mackey and Currie 2001).

It appears that despite the enormous attention the IDH has received, there still remains considerable confusion about the role of disturbance in promoting coexistence (Dial and Roughgarden 1998; Sheil and Burslem 2003). Even though profoundly criticised, the IDH remains a useful conceptual framework incorporating a variety of interwoven mechanisms (Collins and Glenn 1997). Recent developments to resolve the dispute involve the mathematical description of mechanisms that are encapsulated in the IDH (Chesson and Huntly 1997; Roxburgh et al. 2004; Shea et al. 2004). Such mathematical approaches still demand verification by empirical studies.

The role of productivity

Parallel to the exploration of the role of disturbance, fluctuating patterns of diversity have long been related to gradients of productivity (Connell and Orias 1964). Similar controversy exists around the productivity-diversity relationship (Mittelbach et al. 2001), concerning its general shape as well as underlying mechanisms (Abrams 1995; Waide et al. 1999).

Productivity-diversity patterns are diverse. Along spatial and temporal gradients of productivity diversity patterns range from linearly increasing or decreasing functions to unimodal, or even no significant relationship (Grime 1973; Abrams 1995; Mittelbach et al. 2001; Worm and Duffy 2003). Yet the unimodal pattern has become an established textbook example and has even been rated among the few valid generalizations in ecology (Huston 1994; Rosenzweig 1995; Waide et al. 1999). To explain the apparent disagreement of patterns, theoretical considerations as well as empirical studies suggest a co-dependence of diversity on other factors, such as geographic, ecological and taxonomic scale (Huston 1979; Hall et al. 2000). Generalizations include that local species richness is often unimodally related to productivity, whereas regional and global richness displays linear patterns (Worm and Duffy 2003). In marine ecosystems, diversity has been claimed to decrease with nutrient enrichment at sites with initially high productivity and to increase with nutrient enrichment at sites with low initial productivity (Hall et al. 2000; Worm et al. 2002). Alternatively, unimodal productivity-diversity relationships in plants have been considered to occur along natural

productivity gradients, while fertilization generally reduces diversity (Rajaniemi 2003). By and large, non-significant relationships prevail in nature and the variability of patterns is high, even within defined categories. It was therefore suggested that a number of coalescent mechanisms underlie the productivity-diversity relationship (Waide et al. 1999).

Different mechanisms can give rise to a unimodal pattern. General consensus exists regarding the low diversity forming the left tail of the hump-shaped pattern. Since few species are adapted to tolerate very low productivity levels, coexistence is determined by evolutionary processes. In contrast, the decrease of diversity forming the right tail of the correlation is thought to be a result of ecological processes, particularly competition. The different hypotheses explaining this phenomenon share the idea that enhancing productivity above a certain (intermediate) level intensifies competition, and thus reduces diversity in favour of few competitively dominant species (Grime 1977; Huston 1979, 1994; Tilman 1982; Tilman and Pacala 1993). Fig. 2 shows that different models give alternative reasons for the effect of productivity on competition (Waide et al. 1999; Mittelbach et al. 2001; Rajaniemi 2003).

Another aspect that jeopardizes the predictability of the productivity-diversity relationship is the difficulty of distinguishing which factor is cause and which is effect. For simplicity, the bidirectional nature of the relationship has mostly been neglected, which resulted in two separate perspectives about the same correlation. On one hand the diversity of a system affects its

Mechanism explaining low diversity in low productivity regime	Mechanism explaining peak diversity at intermediate productivity levels	Mechanism explaining low diversity in high productivity regime	Productivity-Diversity Theory
Dominance of few species that are tolerant to resource stress	Coexistence	Dominance of few species that are superior competitors	***Total Competition Intensity Theory*** (Grime 1977)
Low population growth rates (influenced by disturbances) select for few species	Dynamic equilibrium of growth-limiting and growth-enhancing factors	Faster-growing populations out-compete poor competitors for nutrients	***Dynamic Equilibrium Model*** (Huston 1979, 1994)
Low habitat heterogeneity through nutrient limitation:: best competitors for nutrients dominate	Highest habitat heterogeneity through habitat co-existence: best competitors for microhabitats of specific nutrient/light ratio co-exist	Low habitat heterogeneity through light limitation: best competitors for light dominate	***Habitat Heterogeneity Theory*** (Tilman 1982; Tilman & Pakala 1993)

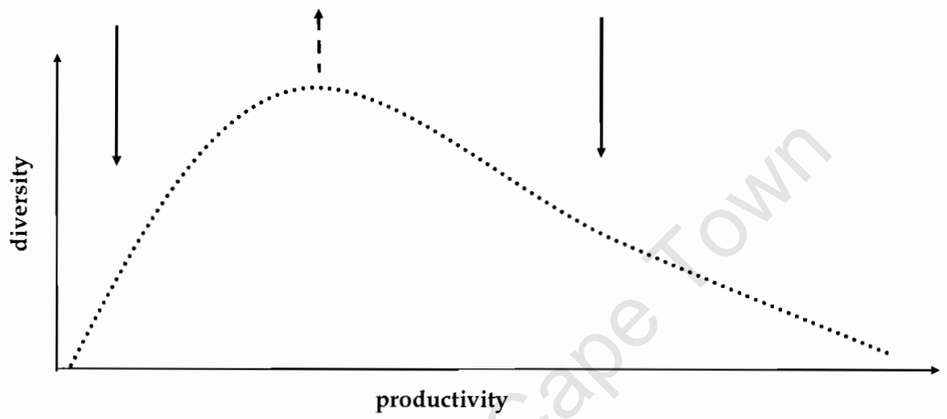

Figure 2: The unimodal relationship between productivity and diversity. Various hypotheses are captured that explain the decline of species diversity in low and high productivity regimes and why peak diversity occurs at intermediate levels of productivity. Note that the *Dynamic Equilibrium Model*, incorporating both productivity and disturbance, is depicted as mirror image to figure 1, reflecting their opposing forces on a community.

productivity. More diverse (plant) communities are known to be more productive (Darwin 1859; Naeem et al. 1994; Tilman et al. 1996), since interspecific differences in the utilization of nutrients allow a more efficient use of limiting resources (Tilman and Downing 1994; Naeem and Li 1997). On the other hand ample evidence exists that changes in a system's productivity affect its diversity (Waide et al. 1999). Changes are often induced by altered nutrient availability, such as by eutrophication. However, real productivity-diversity relationships may work bi-directionally and involve feed-back loops and indirect effects (Worm and Duffy 2003). Such complex webs of mechanisms (Waide et al. 1999) might be the cause of the apparent chaos of observed diversity patterns.

Interactions between disturbance and productivity

It is now evident from theoretical as well as empirical investigations that neither disturbance nor productivity gradients independently account for the celebrated unimodal patterns of diversity. The complex interactions between diversity, productivity and disturbance require a multivariate approach to disentangle causes and effects and become predictive about changing patterns of diversity (Fig.3).

An early theory incorporating the interactive effects of disturbance and productivity on diversity is Huston's *Dynamic Equilibrium Model* (Huston 1979, 1994). It is based on the idea that the coexistence of competing species depends on factors that influence the rate of competitive displacement.

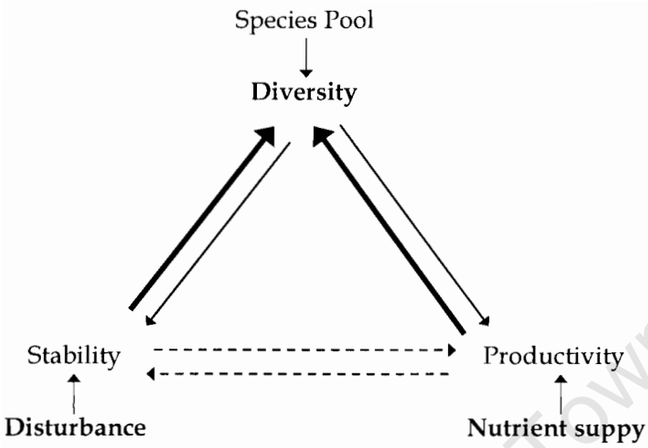

Figure 3: The bidirectional relationships between disturbance, productivity and diversity, showing the potential complexity of interactions by indirect effects and feed-back loops (adapted from Worm and Duffy 2003). Dashed arrows indicate hypothetical relationships. Bold arrows point out which aspects I specifically address in this study.

Diversity is expected to be high in communities with low rate of competitive displacement and vice versa. Both disturbance and productivity influence the rate of competitive displacement - with opposing effects. Productivity directly affects population growth rates and thus rates of competitive displacement. Increasing productivity is therefore expected to reduce diversity. In contrast, disturbances slow down net population growth and thus reduce rates of competitive displacement. In this fashion the opposing forces of productivity and disturbance reach a dynamic equilibrium, and so jointly shape diversity. In essence, the degree of disturbance that maximizes diversity increases as productivity increases (Hastwell and Huston 2001) and vice versa.

More recently, Kondoh (2001) developed a model to clarify the interaction of productivity and disturbance, as proposed by the *Dynamic Equilibrium Model*. Based on a trade-off between competitive ability and colonisation rate (like the IDH), Kondoh's model predicts that if disturbance is high and productivity is low, then species that are better colonizers but interior competitors dominate and diversity is low. In contrast, if disturbance is low and productivity high, species that are superior competitors but poor colonizers out-compete other resource users, and diversity is also low. Peak diversity is expected when both productivity and disturbance are intermediate, and species composition is balanced between superior competitors and better colonizers. Hence, Kondoh's model can be applied to test both disturbance-diversity and productivity-diversity relationships. Increasing disturbance can lead to a monotonic decrease of diversity when

productivity is low and to a monotonic increase when productivity is high. Conversely, gradually enhancing productivity can augment diversity under high disturbance and reduce diversity under low disturbance. Hump-shaped patterns for both relationships are only expected when the respective other factor is at intermediate levels (Fig. 4).

The proposed interplay of disturbance and productivity has been confirmed by some empirical studies (Wilson and Tilman 1993; Gough and Grace 1998; Proulx and Mazumder 1998; Worm et al. 1999; Hall et al. 2000; Worm et al. 2002). Often the approach has been to explain a discrepancy of patterns by post-hoc identification of interacting factors. However, experiments with gradients of both disturbance and productivity to examine the suggested trends in their interactions are rare (Collins and Glenn 1997).

To test Kondoh's interpretation of the *Dynamic Equilibrium Model*, I conducted a two-factorial field experiment by generating gradients of both disturbance frequency and nutrient availability and observing the associated changes in diversity and community structure. Working on a subtropical intertidal rocky shore, I specifically addressed the following questions:

1. Does the IDH explain species coexistence?
2. If not, can the IDH be rejected? Are its assumptions met?
3. Do nutrient additions affect community structure and diversity?
4. Does the response of community structure and diversity to disturbance depend on background nutrient levels?

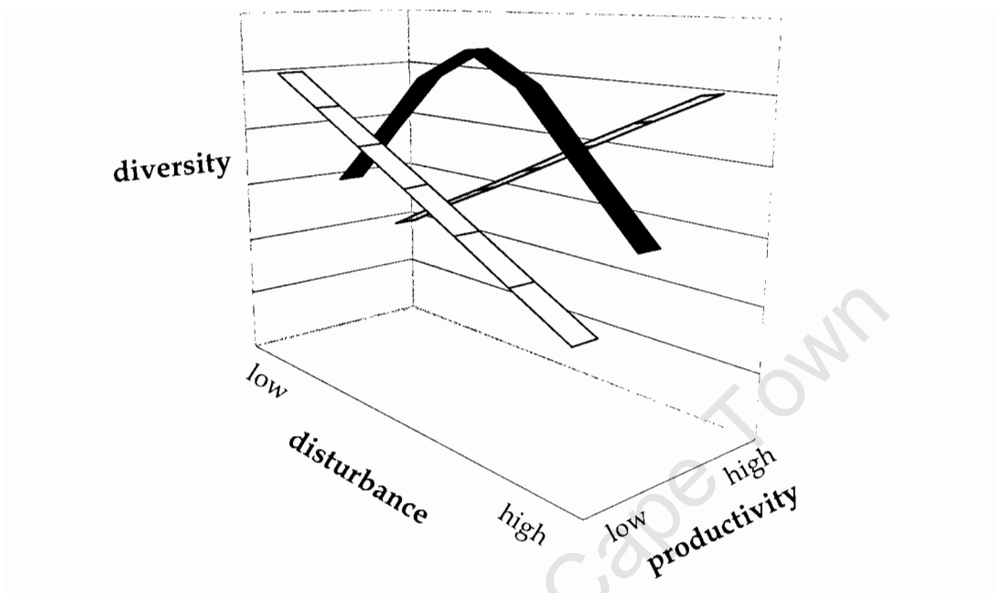

Figure 4: The interactive effects of disturbance and productivity on diversity (adapted from Kondoh 2001). My study aimed to test the proposed model by generating gradients of disturbance (7 levels) and productivity (3 levels) and observing their effect on diversity.

5. If yes, do the interactive effects of disturbance and productivity produce diversity patterns as predicted by Kondoh's model?

METHODS

I conducted a 2-factorial field experiment to test for the interactive effects of disturbance frequency and nutrient availability on species diversity in macrobenthic intertidal rocky shore communities.

Study sites

The experiment was set up on the north-east coast of South Africa in the Maputaland Marine Protected Area (Fig. 5). The two proximate study sites "Lala Nek" (27° 13′ 25.8″ S, 32° 47′ 44.1″ E) and "Mabibi" (27° 20′ 02.2″ S, 32° 45′ 10.3″ E) are semi-exposed rock points emerging above sea level at low tides. They consist of broken plateaus of quaternary sandstone that extend parallel to the shore and so give rise to relatively sheltered bays during low tides, while waves break upon them during high tides. Local tides are semidiurnal with mean tidal height of approximately 2 m. Sandy beaches dominate the adjacent coastline. Sand dynamics are known to significantly influence benthic communities by inundation and scouring (Sink 2001). Periodically, the Maputaland shoreline experiences storms and strong swell from remote cyclones. Oligotrophic conditions have been documented offshore (Meyer et al. 2002) and coastal productivity is generally low (Bustamante et al. 1995). Offshore seawater temperatures range between 22 and 27 °C (Sink 2001). Biogeographically, Maputaland rocky shores belong to the tropical Indo-West Pacific region (Jackson 1976; Sink 2001).

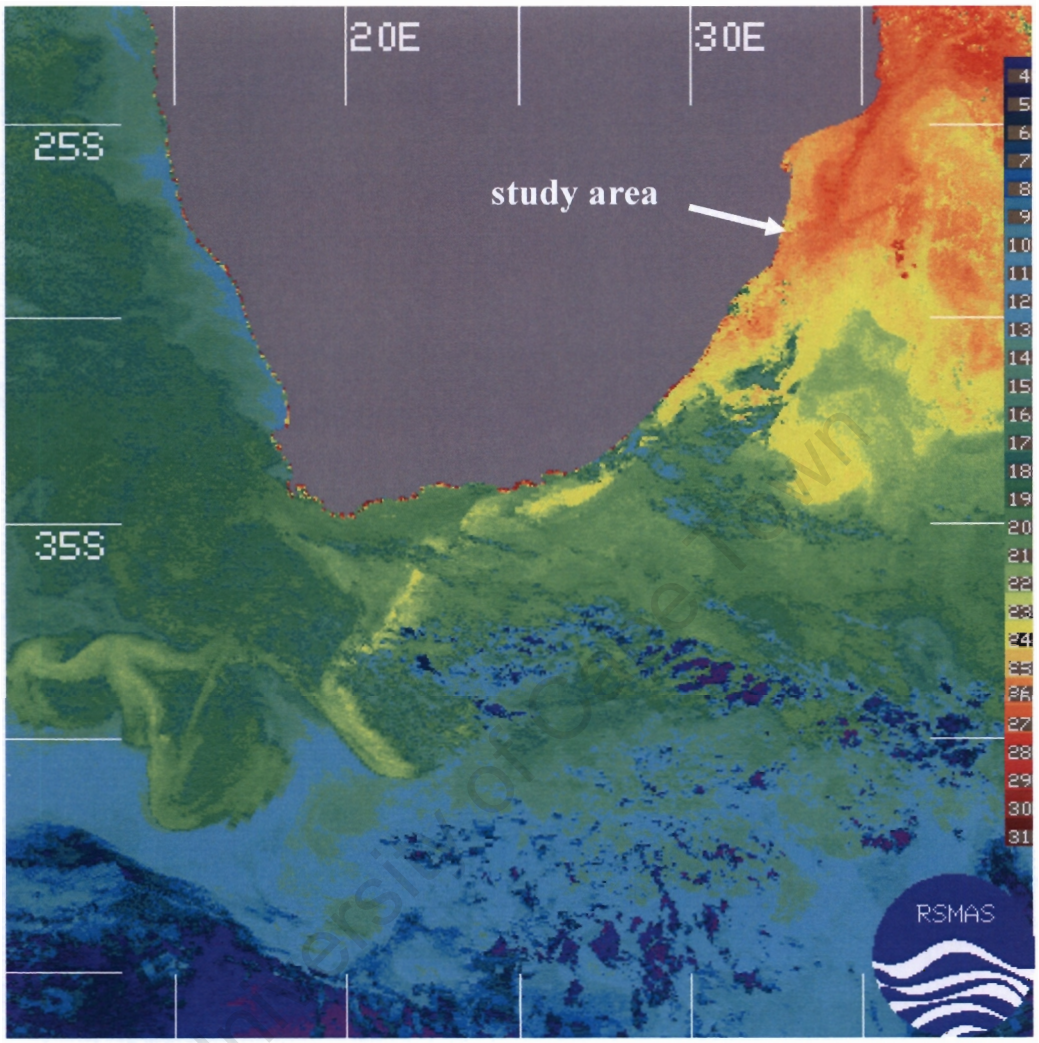

Figure 5: Satellite image of sea surface temperature around South Africa on 29 December 2003 (Global Area Coverage resolution daily image composite).The arrow points to the study area in the Maputaland Marine Protected Area, which is situated in the far north-east of KwaZulu-Natal province. The oceanographic conditions at the study sites are governed by the warm southward flowing Agulhas Current. (Image source: Rosenstiel School of Marine and Atmospheric Science Institute http://www.rsmas.miami.edu)

The experiment was placed in the lower mid-shore of the intertidal zone, falling dry for up to three hours during spring low tide. In this zone mixed algal turfs, colonial ascidians, barnacles, sponges, reef-building worms, and zooanthids dominate the macrobenthos.

Experimental phases

The experiment ran 9 months from August 2003 to April 2004. Initially the experimental units were left in the field for 3 months without manipulation, during which time early successional assemblages became established. In the following 6 months of the treatment phase I manipulated nutrient levels and disturbance frequencies, and recorded community responses to the treatment at 2-monthly intervals (3 sampling sessions).

Experimental design

The experiment followed a modified 2-factorial split-block-design with nutrient enrichment and disturbance as fully orthogonal treatments (Underwood 1997). Seven levels of disturbance frequency were combined with 3 nutrient enrichment levels. The 21 treatment combinations were established in 12 spatial blocks, such that each nutrient enrichment level was replicated in 4 blocks. The blocks represented a random factor, nested in nutrient enrichment level. To account for possible spatial effects of the treatment response, an extra replicate for 2 treatment combinations was added to each block (Fig. 6). In total, every treatment was thus replicated 5

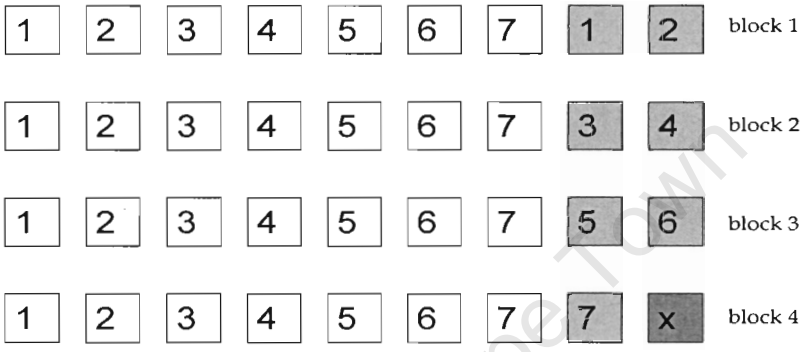

Figure 6: Allocation of 7 disturbance treatment levels on 4 blocks that made up one of the three productivity levels. Replication of treatments between blocks was 4-fold (white), plus one additional within-block replicate (light grey). The extra random replicate (x) was excluded from the analysis. Note: For clarity a consecutive order of disturbance treatments is shown, but the spatial order of treatments was randomly assigned in the field.

times (4 between blocks, 1 within block). Total number of experimental units was 105. Three extra random replicates (x) were included to ensure the spatial consistency of blocks.

Experimental set-up

To maximize the effect of nutrient additions I chose the more wave sheltered side of the rocky headlands with relatively low water movement to position the 12 blocks of the experiment. Minimum distance between the blocks was 5 m. Each block consisted of a horizontal row of 9 experimental units (hereafter EUs). Distance between EUs was 5 cm, within which I attached fertilizer or control bags for the nutrient manipulations. Each EU consisted of a 15x17 cm grey polypropylene panel (thickness 3 mm), roughened by manually sanding with 60pt sand paper for 5 minutes. Each panel was fastened to the rock by 2 stainless steel bolts, nuts and fender washers. A 1-cm gap was left between panel and rock to reduce the impact of benthic grazers. The inclination of the panels was < 40° to the horizontal plane.

Nutrient enrichment

Each EU was positioned between 2 bags of nylon shade cloth (80%, 1 mm mesh size) filled with either 62.5 g (low enrichment) or 125 g (high enrichment) of fertilizer. The corresponding quantitative enrichment levels were to be obtained from regular *in situ* nutrient measurements for the water column adjacent to each block. I used controlled-release fertilizer granules of

nutrient ratio N : P : K = 1 : 0.6 : 1 (Plantacote® pluss 6M, Aglucon Düsseldorf, Germany), as recommended for water column enrichment by Worm et al. (2000). The fertilizer was soaked in water for 14 days prior to placement in the field to ensure maximum release rate as specified by the producer. Fertilizer bags were changed monthly. To control for treatment artifacts I attached bags filled with plastic granules next to unfertilized EUs.

Nutrient measurements

To test for the effectiveness of the nutrient enrichment, seawater samples taken adjacent to blocks were regularly analyzed for their nitrate, phosphate and chlorophyll *a* content. Samples were taken fortnightly throughout the treatment phase at one site (Lala Nek), and at the beginning and end of the treatment phase at the other site (Mabibi). I collected 500 ml of water at each of the blocks (with a specific nutrient level), pooled from smaller amounts taken < 5 cm above each EU. The water was filtered using Whatman GF/F or equivalent Advantec GF 75 glass fiber filters. Subsequently samples and filters were frozen at -20°C within 6 hours of sampling and kept in the dark until analysis. Ortho-Nitrate and Ortho-Phosphate concentrations were determined by autoanalysis within 6 weeks of sampling. For nitrates a *Perstorp autoanalyzer* (cadmium reduction method; Grasshoff 1983) was employed, for phosphates a *Technicon AA 11* (ascorbic acid reduction method; Koroleff 1983). Chlorophyll *a* concentrations were determined for 9 blocks (n=3) per site. Glass fibre filters were used to capture the microalgal content of

500ml seawater samples, and chlorophyll *a* was analyzed within 6 weeks of sampling using a Turner Design 10-AU fluorometer (narrowband, non-acidification method; Welschmeyer 1994).

Disturbance frequencies

A disturbance event was defined as random removal of 20% of the biotic cover on an EU. The treatment consisted of clearing two circular patches of 10% cover each with a paint scraper. The time interval between such disturbance events varied between the different treatments: the seven disturbance levels included an undisturbed control and disturbance events every 12th, 10th, 8th, 6th, 4th and 2nd week).

Data capture

Every second month during the treatment phase species cover on all EUs was recorded by non-destructive sampling in the field using a 6x magnifying glass. Percentage cover of all sessile species >1 mm (as well as colonies of unicellular organisms that form unique structures >1 mm) was estimated with 5% resolution. Rare species were assigned a value of 1%. To avoid edge effects, I excluded a 1-cm margin along the edge of each EU and around the fender washers. Wherever possible the organisms were identified to species level. In most other cases I could identify the organisms to genus, in one case only to family (Ectocarpaceae). Due to the non-destructive protocol it is possible that a number of similar looking species were pooled (within genera such as *Ulva*, *Enteromorpha*, *Sargassum*). To record unidentified species, such

as encrusting algae (J. Bolton and R. Anderson pers. comm.), I used descriptive names.

For each EU, species richness and Pielou evenness were determined. After completion of the treatment phase the biotic dry mass on each EU was measured by scraping the growth off each panel (excluding a 1-cm margin at the edges) and drying it at 60°C until constant weight was reached ($\Delta < 1$ g). Not all sand could be excluded from the turf-like algal mats, which might have led to an overestimate of dry mass.

To quantify a possible effect of sand dynamics on community structure (McQuaid and Dower 1990; Sink 2001), sand cover was monitored on and around individual panels as often as possible. Six categories (0-5) were specified: 0 = no sand on panel or within 1m; 1 = no sand on panel, but sand within 1m; 2 = sand touching panel or sand film (< 1 mm) on panel; 3 = sand partly covering (>1 mm) panel; 4 = sand completely covering panel (< 1 cm); 5 = sand completely covering panel (>1 cm). The mean score per plate served as factor for the multivariate analysis of community structure.

Data Analysis

Nutrient enrichment

To test for effective nutrient enrichment of the seawater around the EUs, a repeated-measures analysis of variance (ANOVA; Statistica 5.0) was employed to compare nutrient and chlorophyll concentrations from different enrichment levels over time.

Biological response to the treatment

Data from the final sampling session were examined for the effects of the disturbance and nutrient treatments on univariate response variables (species richness, evenness, dry mass, total biotic cover) using ANOVA, and the effects on multivariate species-cover data (i.e. community structure) using ANOSIM and SIMPER analyses (PRIMER 5.2.2).

Prior to the univariate analyses, the data were balanced to increase the robustness of the tests. Balancing involved either (a) the substitution of missing EUs by virtual EUs that carried treatment-specific mean values of the response variables or (b) randomly discarding extra EUs (Underwood 1997). I balanced the data based on the following considerations: At Mabibi, 11 of 105 EUs were lost in the course of the experiment, including a whole block. Balancing could therefore involve (a) the calculation of 11 virtual EUs (+10.5%), or (b) the random removal of 10 EUs (-10.6%). The first option (a) would imply considerably reducing the variance within treatment groups, thereby increasing the chance of committing a type II error in an ANOVA (i.e. failure to detect a significant difference where there was one). Simultaneously, the higher total number of EUs (due to addition of virtual EUs) and resulting higher degrees of freedom would have increased the chance of making a type I error (i.e. detection of a significant difference where there was none). The second option (b) can also lead to a decrease of the variance if extremes are removed, and thus the chance of committing a type II error also exists.

Moreover this chance gets amplified by the reduction of EUs and degrees of freedom. I therefore decided to balance by using option (a), where the increased chance of a type II error (reduced variance) gets balanced with the increased chance of a type I error (higher degrees of freedom).

In cases of heteroscedascity of variances (Cochran's test $p < 0.05$) data were log-transformed. When none of the standard transformations produced equal variances, significant results were re-evaluated with reference to post-hoc comparisons and graphic representations of the data to control for the increased chance for a type I error. Data for percentages of total biotic cover were arcsin-transformed prior to analysis.

Based on the modified split-block design of the experiment, I performed 2-way nested ANOVA with factors nutrients (N), disturbance (D), and block nested in nutrients B(N) to test for significant treatment effects on species richness, evenness, dry mass and total biotic cover. The mathematical model I employed to explain the variance from the mean with respect to treatment effects was:

$$X_{ijkl} = \mu + N_i + D_j + B(N)_{k(i)} + B(N) * D_{j(i)k} + N * D_{ik} + \varepsilon_{lj(i)k};$$

where *i* refers to nutrient level, *j* to disturbance level, *k* to block and *l* to EU;

X is the observed magnitude of the response variable;

μ is the overall mean of the response variable;

N, *D* and *B* represent the variance explained by the nutrient treatment, disturbance treatment, and spatial position (block) respectively;

ε signifies the unexplained variance, or residual (Underwood 1997).

The products denote interactions of particular effects.

Brackets symbolize nested factors.

In some cases I increased the test power of the ANOVA by manually recalculating the F-ratio using the (smaller) residual variance ε as denominator rather than the within-group variance of the classical model. Conceptually this means that the variance between different treatment groups (among-groups variance) was measured relative to the variance between EUs that experienced identical treatment regarding nutrient and disturbance levels as well as positioning on the same block (within-block variance). In contrast, the classical approach measures the treatment effects (among-groups variance) against the variance within a group of equal treatment regardless of spatial positioning on different blocks (within-group variance). Such within-group variance is expected to be higher than the within-block variance ε. As a result, the F-ratio calculated with the residual ε as denominator is higher, which in turn increases the probability of a significant treatment response. Increasing test power with the described method of "pooling" must be handled with caution, since it increases the risk of committing a type I error (Underwood 1997). The assumption of pooling is that there is no variance between spatial replicates or, rather, that the treatment effect is not dependent on the spatial positioning, i.e. that there is no interaction between spatial (block) and treatment effects. Therefore, to detect hidden disturbance effects I only pooled in the case of a highly insignificant ($p > 0.25$) interaction between the factors block and disturbance. To detect hidden nutrient effects by

pooling, a highly insignificant block effect was a prerequisite (as no interaction was possible due to nesting)(L. Benedetti-Cecchi, pers. comm.).

Post-hoc tests were made for significant effects using *Ryan's Q Test* to compare between disturbance levels (recommended as most powerful test for all pairs comparisons) and the *Student-Newman-Keuls Test (SNK)* (stronger power, but unsuitable for > 3 treatment levels) or *Dunnet T3 test* (for heterogeneous variances) to contrast nutrient levels (Day and Quinn 1989). Multivariate species-cover data were compared by using ANOSIM (Bray-Curtis Similarity co-efficient) and SIMPER analyses, as offered by PRIMER. Due to significantly different community compositions at the two study sites, all subsequent analyses were performed separately per site. Two-way crossed ANOSIMs for factors "nutrients" and "disturbance" were performed to assess treatment effects. Since there was no effect of "disturbance" on community structure (see below), the test power for "nutrient" effects could be increased through 1-way analysis. Additionally, 1-way ANOSIM for factors "block" and "sand cover" (separate for each productivity level) were employed to identify spatial heterogeneity and a possible determinant thereof.

RESULTS

Site differences

Community structure was significantly different between the two sites Mabibi and Lala Nek (1-way ANOSIM; R = 0.767: $p < 0.001$; Fig. 7). SIMPER analysis showed 90.17% average dissimilarity between the species assemblages, largely explained by the dominance of the turf-forming algae, such as *Cladophora coelotrix* and *Centroceras clavulatum* at Mabibi, as opposed to crustose life forms, such as "Encrusting alga light brown" and the barnacle *Tetraclita squamosa rufotincta* at Lala Nek (Table 1; Fig. 8). Consequently, all further analyses were done separately for each site.

Spatial heterogeneity

Spatial heterogeneity among blocks of equal nutrient treatment was generally high, as reflected in the prevailing "block" effects in univariate (Table 2) as well as multivariate analyses (Table 3). Additionally, total species richness per site was much higher (Mabibi: 39; Lala Nek: 34) than the mean species richness on single EUs (Mabibi: 7.4; Lala Nek: 5.3), indicating within-site differences among EUs. Differences in mean sand cover during the treatment phase did not consistently coincide with differences in community structure, whereas the ubiquitous "block" effects reflected the general patchiness of the intertidal system.

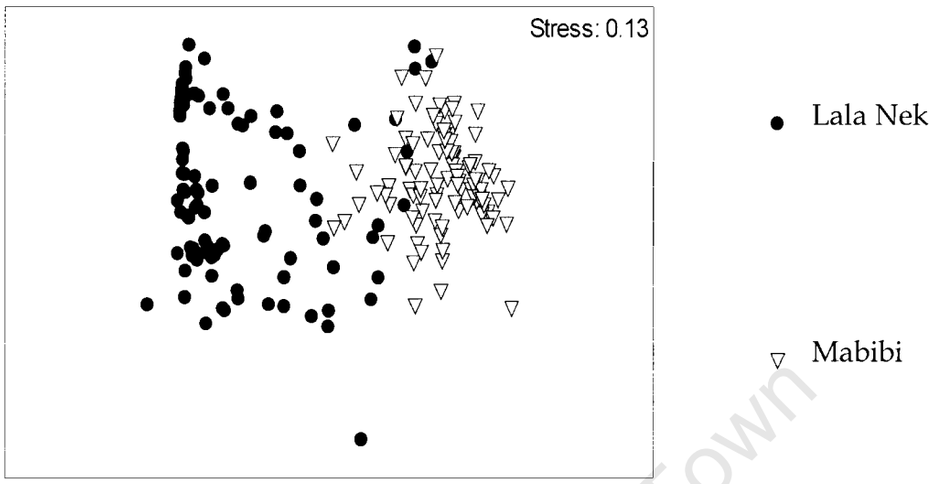

Figure 7: Ordination plot (Multidimensional Scaling) showing marked differences (90.17 %) between species assemblages at Lala Nek and Mabibi.

Table 1: The most important species accounting for the significant difference between the two sites Mabibi and Lala Nek, as identified by SIMPER analysis (using Bray-Curtis dissimilarities).
S = within-site similarity; Ave % cov = average % cover of species; Ave diss = average dissimilarity of a species between sites; Diss/SD = ratio of mean/standard deviation of dissimilarity of a species as measure of spread or consistency of dissimilarity; % (cum.) Contr. = % (cumulative) contribution of species to the dissimilarity between sites.

	Mabibi (S=48.37)	**Lala Nek (S=33.41)**				
Species	**Ave % cov**	**Ave % cov**	**Ave diss**	**Diss/ SD**	**% Contrib.**	**% Cum. contrib.**
Cladophora coelothrix	29.76	0.96	24.79	1.39	27.49	27.49
Encrusting alga "light brown"	1.56	26.73	19.1	0.96	21.18	48.67
Centroceras clavulatum	21.86	4.27	17.9	1.27	19.86	68.53
Unidentified Ectocarpaceae	9.19	2.5	7.76	1.09	8.61	77.14
Tetraclita squamosa rufotincta	0.08	4.43	4.23	1.24	4.69	81.83
Padina boryana	2.81	0.09	2.49	0.87	2.76	84.59
Dictyota humifusa	1.61	0.14	1.43	0.39	1.59	86.18
Encrusting alga "dark brown"	0.11	1.4	1.37	0.41	1.52	87.69
Encrusting coralline alga "pink"	1.4	0.34	1.32	0.65	1.47	89.16
Ulva spp.	1.25	0.26	1.22	0.7	1.35	90.51

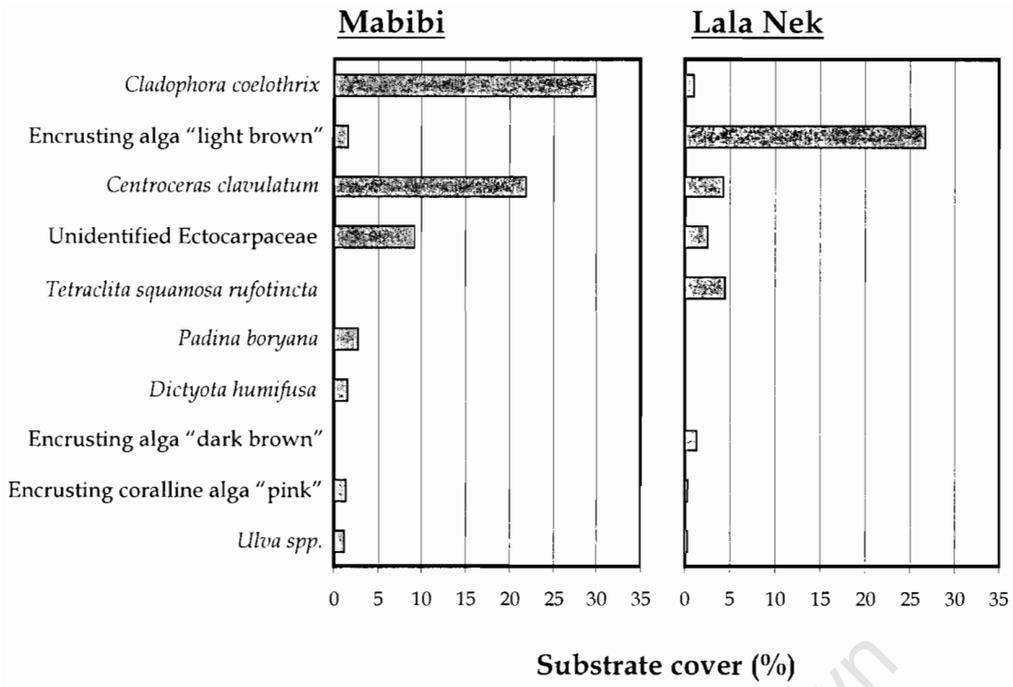

Figure 8: Differences of the species assemblages at the sites Mabibi and Lala Nek. Average percentage cover of the most determining species is shown, with the relative contribution to the between-site difference decreasing from top to bottom (see Table 1).

Table 2: Results of 2-way nested ANOVA of species richness, evenness, dry mass and total biotic cover at the two sites Mabibi and Lala Nek. The model accounts for effects of "block" *b* (i.e. spatial position, nested in "nutrients"), "nutrient" level *n*, "disturbance" frequency *d*, as well as their interactions. Bold numbers indicate significant effects ($p < 0.05$).
$_1$: log transformed; $_2$: *F*-value recalculated using residual as denominator; $_3$: heteroscedacity of variances even after transformation.

		MABIBI				LALA NEK			
Response variable	**Source**	**df**	**MS**	**F**	**p**	**df**	**MS**	**F**	**p**
Species richness	**block (b)**	9, 21	18.64	6.44	**0.0002**	9, 21$_1$	0.29$_1$	21.25$_1$	**<0.0001**$_1$
	nutrients (n)	2, 9	38.55	2.07	0.1824	2, 9$_3$	201.38$_3$	5.46$_3$	**0.028**$_3$
	disturbance (d)	6, 54	4.29	1.68	0.1445	6, 54$_1$	0.01$_1$	0.38$_1$	0.8896$_1$
	b x d	54, 21	2.56	0.88	0.6523	54, 21$_1$	0.02$_1$	1.23$_1$	0.3093$_1$
	n x d	12, 54	1.99	0.78	0.6703	12, 21$_{1,2}$	0.03$_{1,2}$	2.28$_{1,2}$	**0.0476**$_{1,2}$
Evenness	**b**	9, 21	0.02	1.27	0.3086	9, 21	0.29	18.76	**<0.0001**
	n	2, 9	0.09	4.82	**0.0377**	2, 9	0.32	1.09	0.3756
	d	6, 54	0.01	1.18	0.3292	6, 54	0.08	4.09	**0.0018**
	b x d	54, 21	0.01	0.65	0.8966	54, 21	0.02	1.22	0.3166
	n x d	12, 54	0.02	1.76	0.0801	12, 54	0.01	0.52	0.8957
Dry mass	**b**	9, 21$_3$	1659.18$_3$	8.71$_3$	**<0.0001**$_3$	9, 21	288.61	1.72	0.1460
	n	2, 9	4600.68	2.77	0.1153	2, 9	1745.18	6.05	**0.0216**$_3$
	d	6, 54	329.43	1.31	0.2700	6, 54	59.49	0.83	0.5530
	b x d	54, 21	252.08	1.32	0.2433	54, 21	71.79	0.43	0.9935
	n x d	12, 54	243.77	0.97	0.4908	12, 54	43.27	0.60	0.8303
Total biotic cover	**b**	9, 21$_3$	518.88$_3$	5.46$_3$	**0.0007**$_3$	9, 21	1642.14	14.40	**<0.0001**
	n	2, 9	1049.73	2.02	0.1881	2, 9	938.00	0.57	0.5841
	d	6, 54	106.22	1.43	0.2194	6, 54	286.55	3.47	**0.0057**
	b x d	54, 21	74.15	0.78	0.7716	54, 21	82.62	0.72	0.8297
	n x d	12, 54	175.85	2.37	**0.0155**$_3$	12, 54	114.46	1.39	0.2015

Table 3: Results of multivariate ANOSIM of community structure. Treatment effects of nutrient enrichment (levels N0 = unfertilized; N1 = low enrichment; N2 = high enrichment) and disturbance frequency (levels D1 = undisturbed, to D7 = disturbed every 2nd week) were identified with 2-way crossed design. Test power was increased *a posteriori* for nutrient effects by 1-way analysis. Spatial effects of blocks (B1 to B12) and mean sand cover (levels S0 = no cover to S3 = mostly covered) were assessed for individual nutrient levels with 1-way analyses. Bold font indicates significant differences ($p < 0.05$).

data subset	ANOSIM design	factors	significant pairwise differences ($p < 0.05$)	R	p
both sites	1-way	**site**	**(Lala Nek,Mabibi)**	**0.767**	**0.001**
Mabibi – all data	2-way crossed	**nutrients** disturbance	**(N0,N1)(N0,N2)** **(D2,D5)**	**0.101** - 0.026	**0.014** 0.740
Mabibi – all data	1-way	**nutrients**	**(all,all)**	**0.135**	**0.001**
Mabibi – nutrient level 0	1-way	**block**	**(B1,all)**	**0.246**	**0.001**
	1-way	**sand cover**	**(S2,S3)**	**0.33**	**0.004**
Mabibi – nutrient level 1	1-way	**block**	**(all,all)**	**0.57**	**0.001**
	1-way	sand cover	-	0.093	0.131
Mabibi – nutrient level 2	1-way	**block**	**(all,all)**	**0.341**	**0.001**
	1-way	sand cover	-	0.097	0.198
Lala – all data	2-way crossed	**nutrients** disturbance	**(N0,N2)(N1,N2)** **-**	**0.138** - 0.043	**0.001** 0.893
Lala – all data	1-way	**nutrients**	**(all, all)**	**0.181**	**0.001**
Lala – nutrient level 0	1-way	**block**	**(B4, all)(B6,B12)**	**0.438**	**0.001**
	1-way	sand cover	-	- 0.098	0.814
Lala – nutrient level 1	1-way	**block**	**(all,all)**	**0.57**	**0.001**
	1-way	sand cover	-	0.033	0.313
Lala – nutrient level 2	1-way	**block**	**(all,all)**	**0.57**	**0.001**
	1-way	**sand cover**	**(all,all)**	**0.403**	**0.001**

Maturation

By commencement of the treatment phase (i.e. three months after installment of the artificial substrates in the field) the communities were still developing, since more than 80% of the substrate was bare of biotic cover (i.e. of organisms > 1 mm) and, on average, < 4 species were found per EU. Maximal maturation was reached 4 months after treatment began. Thereafter there was a decline partly caused by a series of storms and extreme low tides that increased mortality (Fig. 9).

Effects of disturbance treatments

The disturbance treatment (D1= undisturbed control, D2-D7 = disturbed every 12th to every 2nd week) only showed effects on some community parameters (Table 2: species richness, evenness, dry mass, total biotic cover; Table 3: community structure), and only at Lala Nek. At Mabibi no significant disturbance-related changes were detected (Fig. 10a-l). At Lala Nek, disturbance frequency did not affect species richness (Fig. 11a-c), dry mass (Fig. 11g-i) or community structure, but significantly influenced evenness (Fig. 11d-f) and total biotic cover (Fig. 11j-l). Evenness increased with increasing disturbance frequencies (regression, $R = 0.2570$, $p = 0.0081$, pooled across all nutrient levels), with post-hoc tests detecting a significant difference between average evenness at control (D1, 0.55 ± 0.24) and high disturbance frequency (D7, 0.76 ± 0.14; Ryan's Q test, $p < 0.05$). In contrast, total biotic cover generally decreased with increasing disturbance frequency (regression,

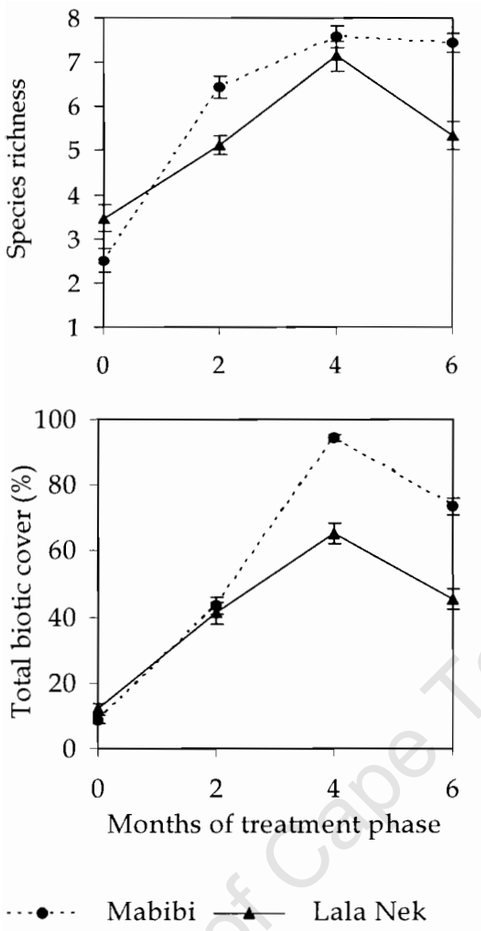

Figure 9: Maturation of communities at Mabibi and Lala Nek with respect to average (± SD) species richness and total biotic cover per experimental unit (panel) during the treatment phase.

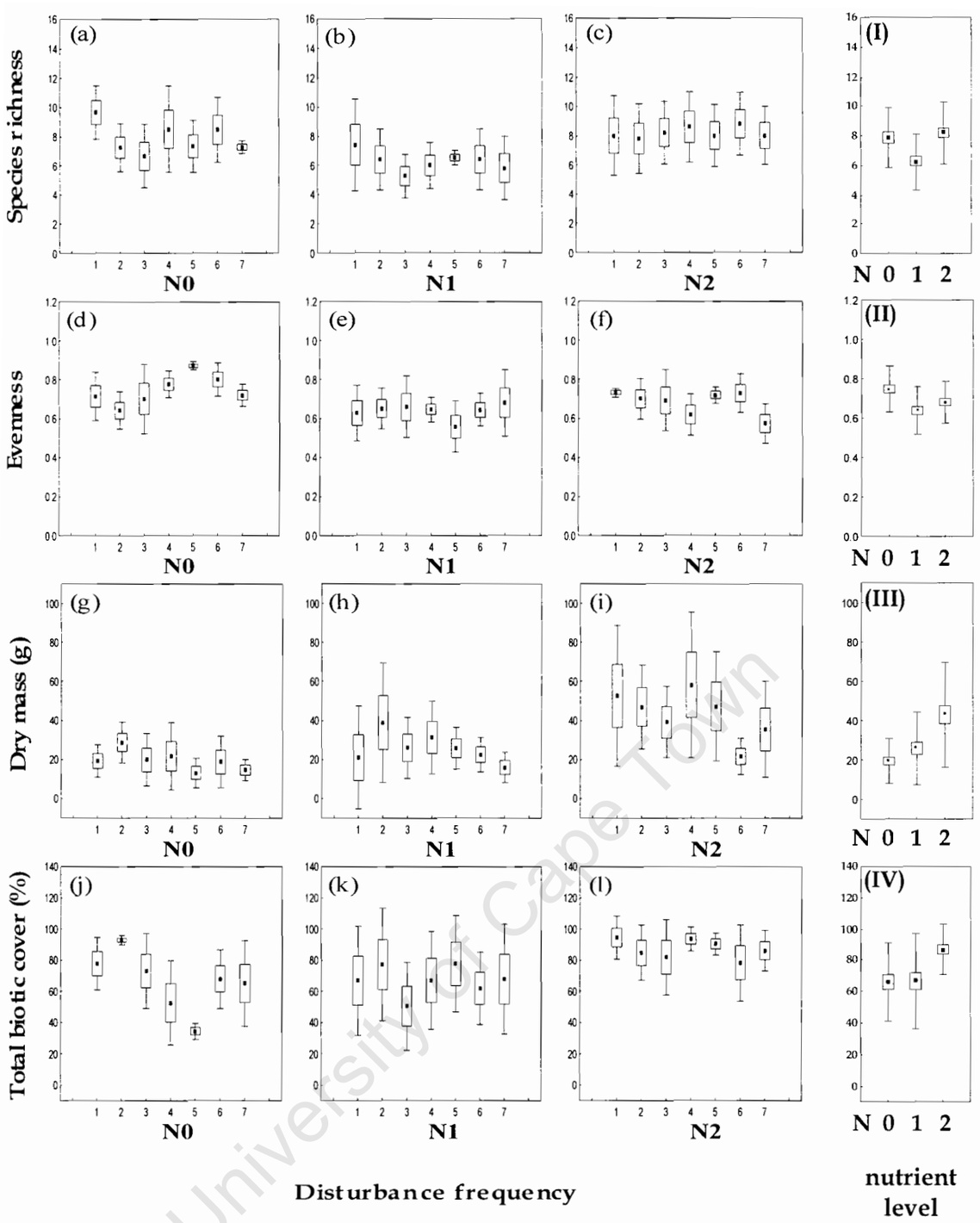

Figure 10: Effects of nutrient enrichment and disturbance frequency on (a)-(c) species richness, (d)-(f) Pielou's evenness index, (g)-(i) dry mass and (j)-(l) total biotic cover at Mabibi. The box-whiskers show standard errors and standard deviations around the means. N0 = ambient conditions, N1 = low enrichment and N2 = high enrichment. The disturbance gradient on the x-axes consists of undisturbed control (1), and disturbance events every 12th, 10th, 8th, 6th, 4th and 2nd week (2-7 respectively). Graphs (I)-(IV) on the right show the data pooled by nutrient level.

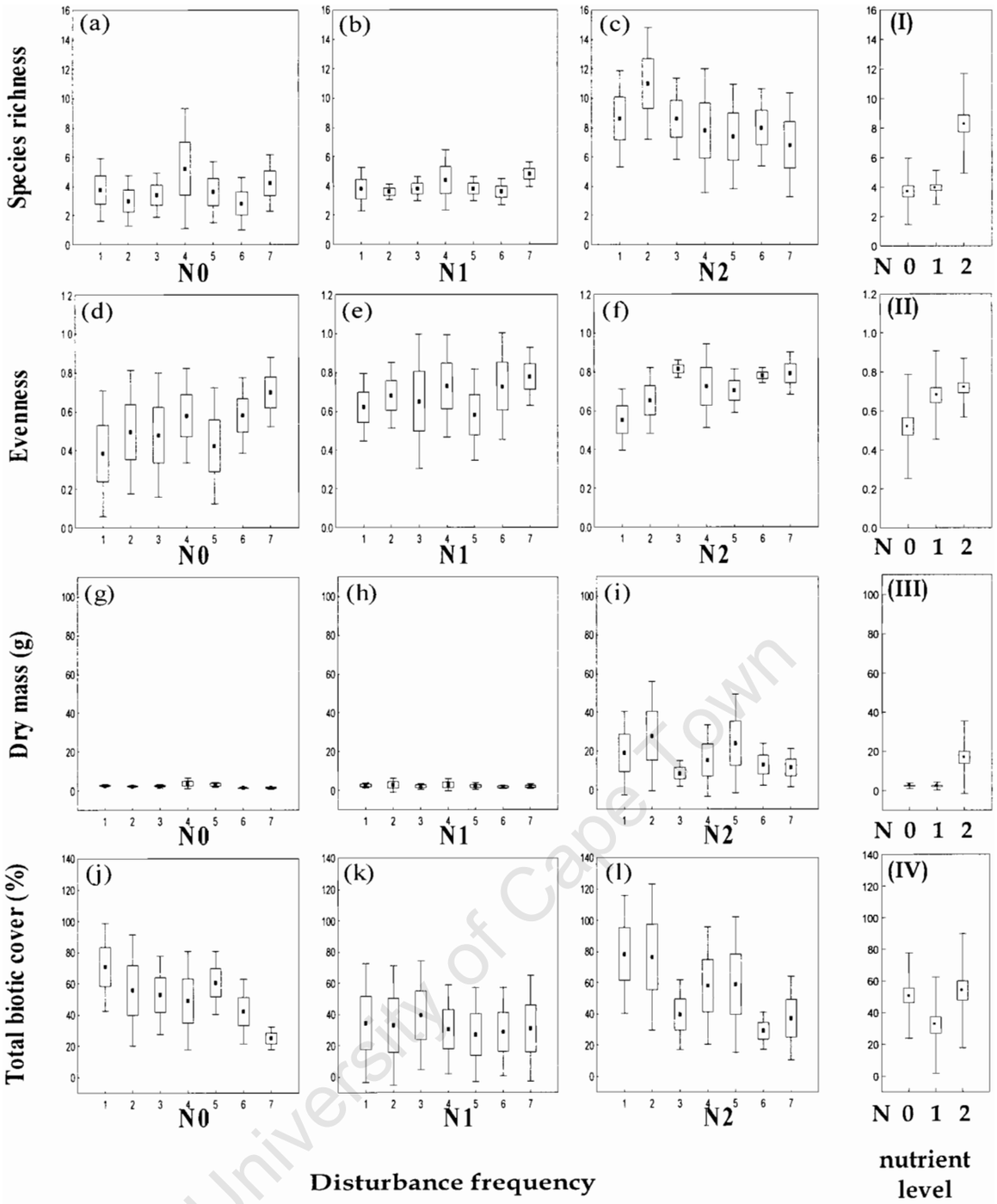

Figure 11: Effects of nutrient enrichment and disturbance frequency on (a)-(c) species richness, (d)-(f) Pielou's evenness index, (g)-(i) dry mass and (j)-(l) total biotic cover at Lala Nek. The box-whiskers show standard errors and standard deviations around the means. N0 = ambient conditions, N1 = low enrichment and N2 = high enrichment. The disturbance gradient on the x-axes consists of undisturbed control (1), and disturbance events every 12th, 10th, 8th, 6th, 4th and 2nd week (2-7 respectively). Graphs (I)-(IV) on the right show the data pooled by nutrient level.

R = 0.2693, p = 0.0055, pooled across all nutrient levels), with post-hoc tests detecting a significant difference between average percentage cover at low (D2, 56.44% ± 39.45) and high disturbance frequencies (D7, 30.93% ± 23.16; Ryan's Q test, $p < 0.05$).

Effects of nutrient treatments

I did not detect effective nutrient enrichment or enhanced primary production in the water column directly (repeated measures ANOVA; NO_3: $F_{2,9} = 1.59$, $p = 0.2563$; PO_4: $F_{2,9} = 1.80$, $p = 0.2193$; chl *a*: $F_{2,6} = 1.45$, $p = 0.3054$). Nevertheless, there were apparent biotic responses on the settlement panels to nutrient additions (N0 = ambient; N1 = low enrichment; N2 = high enrichment) at both study sites (Tables 2, 3).

At Mabibi, the nutrient treatments significantly affected evenness (Fig. 10-II), which was higher at ambient level N0 (mean± SD = 0.75 ± 0.12) than under enriched conditions, but did not differ significantly between N1 (0.64 ± 0.12) and N2 (0.67 ± 0.11; Student-Newman-Keuls tests, $p < 0.05$). Species richness remained unaffected by nutrient additions (Fig. 10-I). Even though not shown significant through ANOVA, mean dry mass and mean total biotic cover did show an increasing trend with nutrient level (Fig. 10-III, IV). Community structure differed significantly among all nutrient levels (1-way ANOSIM) with more pronounced differences between ambient (N0) and enriched levels (N1, N2) than between low (N1) and high enrichment (N2)(2-way ANOSIM; Table 3). Average similarity of species assemblages within specific nutrient

levels was low (N0: S = 44.75; N1: S = 47.23; N2: S = 58.05). All three treatment groups were characterized by the presence of the turf-forming algae *Cladophora coelothrix* and *Centroceras clavulatum*, and an unidentified brown alga of the family Ectocarpaceae. Ninety percent of within-group similarities were based on the relative abundances of these three species, together with the brown alga *Padina boryana* and "Encrusting alga light brown" at level N0. Average dissimilarities between the nutrient treatment groups (57.88% (N0, N1); 54.31% (N0, N2); 48.55% (N1, N2)) were mainly explained by the differences in relative abundance of *Cl. coelothrix* and *Ce. clavulatum* and the Ectocarp (Fig. 12a). Jointly they accounted for 70.81% and 69.61% of the significant differences between enrichment levels N0 and N1 and between levels N0 and N2 respectively. Overall, the biological response to enrichment at Mabibi was most prominent between ambient conditions (N0) and low enrichment (N1). The green alga *Cl. coelothrix* benefited from the nutrient additions, while the red alga *Ce. clavulatum* and the Ectocarp decreased. The consistency of the nutrient effect on individual species was generally low, with maximal $D_i/SD(D_i)$ (i.e. mean/standard deviation of dissimilarity) being 1.38 for changes of *C. coelothrix* between ambient and high enrichment levels.

At the other site, Lala Nek, nutrient enrichment showed significant effects on species richness, dry mass (Table 2) and community structure (Table 3). Cautious evaluation of the significant nutrient effects on species richness and dry mass was necessary due to heterogeneous variances (Cochran's test, $p < 0.05$). Certainly more species coexisted at high enrichment than at the other

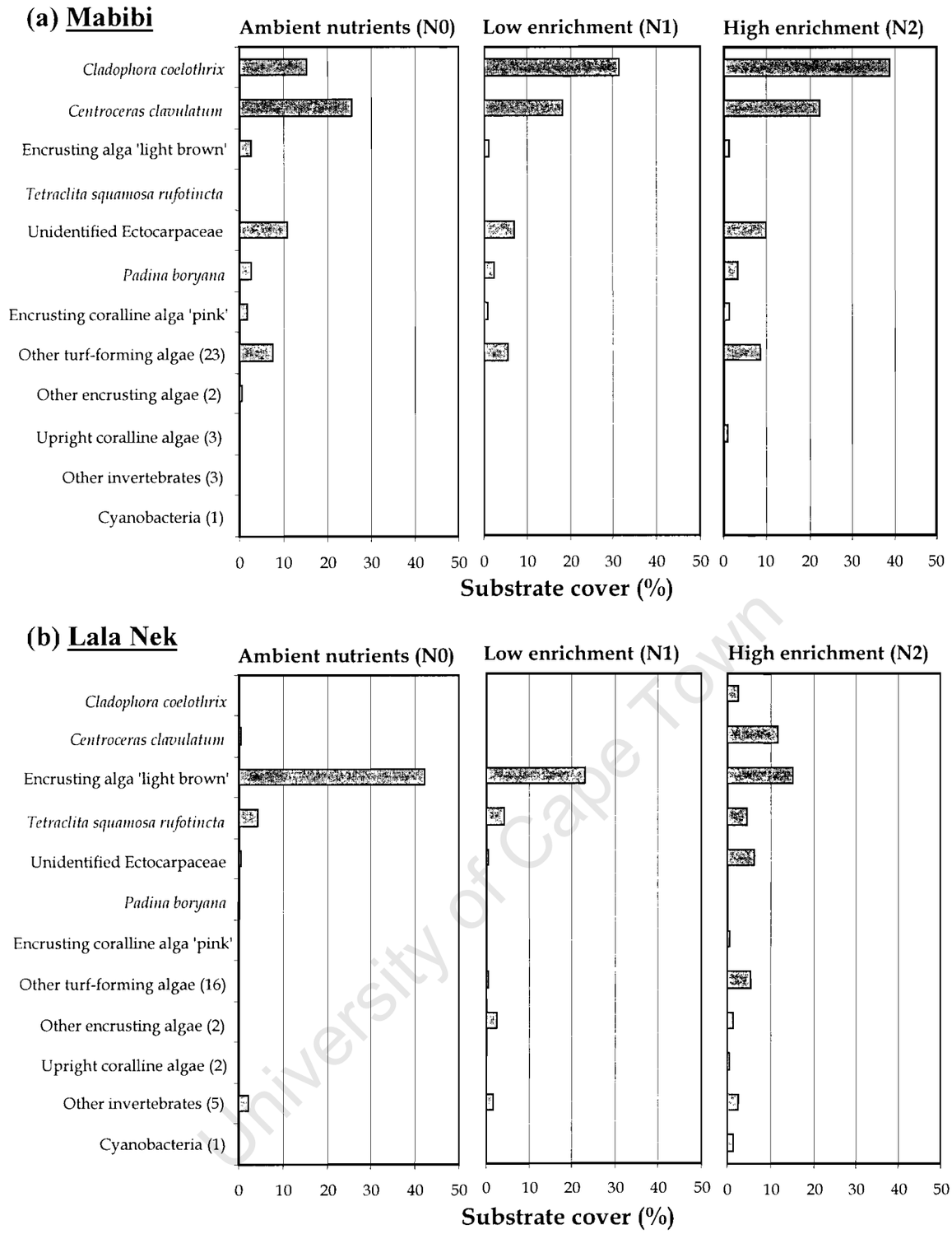

Figure 12: The effect of nutrient enrichment on the average percentage cover of the most characteristic species at Mabibi and Lala Nek. The remaining species were grouped as 'Other turf-forming algae', 'Other encrusting algae', 'Upright coralline algae', 'Other invertebrates' or 'Cyanobacteria' (number of species contained in each category is shown in brackets).

treatments (Fig. 11-I). Dry weight experienced a significant increase under high nutrient enrichment (Fig. 11-III; Dunnet T3 test, $p < 0.05$). The steady increase of evenness with nutrient additions (Fig. 11-II) was not reflected as significant result in the ANOVA (Table 2). However, values for N0 were consistently lower than those for N1 or N2 at all disturbance levels. Analogous to Mabibi, community structure at Lala Nek differed significantly between all nutrient levels (1-way ANOSIM), with the most pronounced change occurring with high enrichment N2 (2-way ANOSIM; Table 3). Average similarity within specific nutrient levels decreased with enrichment and was generally low (N0: S = 50.92; N1: S = 37.79; N2: S = 27.94). All three enrichment levels were characterized by the "Encrusting alga light brown" and the barnacle *Tetraclita squamosa rufotincta*. At enrichment levels N0 and N1 these two species jointly accounted for approximately 90% of within-group similarity, whereas at enrichment level N2 only for 54.27%. Under high enrichment (N2), the algae *Ce. clavulatum*, "Encrusting coralline alga pink" and "Encrusting alga dark brown", together with another barnacle species *Chthamalus dentatus* and the unidentified Ectocarpaceae additionally accounted for 36.77% of the within-group similarity. The pronounced dissimilarities between the nutrient treatment groups N0 and N2 (72.58%) as well as N1 and N2 (73.31%) were chiefly explained by the differences in relative abundance of the "Encrusting alga light brown", *Ce. clavulatum, T. squamosa rufotincta* and the Ectocarp (Fig. 12b). Jointly they explained 71.63% (N0, N2) and 62.27% (N1, N2) of the significant differences. The less obvious

differences between treatments N0 and N1 (61.43%) mostly involved changes in abundance of the "Encrusting alga light brown" and "Encrusting alga dark brown", accounting for 76.62% of the significant differences. Nutrient enrichment led to a substantial decline in the mean abundance of "Encrusting alga light brown". Conversely, *Ce. clavulatum* and the Ectocarp increased considerably under high enrichment (Fig. 12b). However, the consistency of the nutrient effect on individual species was also low at Lala Nek, with by far highest $D_i/SD(D_i)$ being 1.51 for changes of "Encrusting alga light brown" between ambient (N0) and low enrichment (N1) levels. For all other species $D_i/SD(D_i)$ was less than 1, indicating high scatter in the data.

Interactive effects of nutrients and disturbance

At Mabibi, the significant interaction of nutrient and disturbance effects on total biotic cover did not show a consistent pattern, rather indicating a localized difference between disturbance levels D2 and D5 at nutrient level P0 (Ryan's Q test, $p < 0.01$; Fig. 10j-l). This effect may be the result of a type I error due to heterogeneous variances (Cochran's test, $p < 0.05$) and will therefore not be further interpreted.

At Lala Nek, the effect of disturbance frequency on species richness was dependent on nutrient enrichment (significant P x D interaction; Table 2). Only under high enrichment (N2) did increasing disturbance frequency have a negative effect on species richness, whereas no disturbance effect was apparent at ambient (N0) and low (N1) enrichment (Fig. 11a-c).

DISCUSSION

Neither the unimodal relationship predicted by the *Intermediate Disturbance Hypothesis* (IDH) nor any consistent linear disturbance-diversity relationships were detected in this study. One site (Lala Nek) yielded a strong positive relationship between evenness and disturbance, while species richness declined with increasing disturbance frequency only under high nutrient enrichment. This was the only case when disturbance and productivity showed interactive effects on diversity. However, the experiment failed to reproduce the patterns proposed by Kondoh (2001) (Fig. 4). Moreover, no clear response of diversity parameters to disturbance was observed at the other site (Mabibi). The effect of the nutrient treatment also varied between the different species assemblages at the two sites. Nutrient additions consistently affected community structure. However, at Lala Nek these changes were reflected in a significant increase in species richness as evenness increased, whereas at Mabibi evenness decreased with fertilization, while species richness remained unaffected.

Effects of disturbance

Two lines of argument serve to explain that my failure to detect a hump-shaped pattern of species richness along a disturbance gradient does not necessarily lead to the rejection of the IDH. I illustrate (1) that the systems studied did not consistently fulfil the assumptions the IDH is based on, and

(2) how the environmental background may have obscured the response to my disturbance treatment.

Assumptions of the IDH

The systems studied did not consistently fulfil the necessary assumptions of the IDH. Once all prerequisites were met (at Lala Nek under high enrichment) species richness reacted to disturbance according to the prediction.

Essential mechanistic assumptions of the IDH include (1) that species compete for limiting resources; (2) in the absence of disturbance a successional process leads to the dominance of superior competitors; and (3) maximal species diversity occurs at intermediate levels of disturbance, when the majority of inferior competitors succeed in coexisting by opportunistic utilisation of newly available resources (Chesson and Huntly 1997; Sheil and Burslem 2003; Shea et al. 2004). Fundamental for the mechanism to function are certain traits, such as the trade-off that an organism survives either as superior competitor or as quick colonizer (Collins and Glenn 1997) or by being stress tolerant (Dial and Roughgarden 1998). Applying these mechanistic principles of the IDH to benthic rocky shore communities creates the following scenario: (1) space and nutrients are the limiting resources for which sessile organisms primarily compete (Branch 1984; Menge and Branch 2001); (2) in the course of succession superior competitors for space and nutrients will become (spatially) dominant, while (3) weaker competitors only have a chance of coexistence by way of quicker (opportunistic) utilisation of

cleared substrate or available nutrients after periodic disturbance events. Peak diversity is expected at intermediate levels of space-creation, where strong competitors and opportunistic colonizers coexist in patches of different successional age. Since most sessile marine organisms have complex life cycles with planktonic larvae, the re-colonisation of cleared space is partly determined by factors that influence larval availability and settlement (Dayton 1971). Theoretical considerations suggest that the validity of the IDH requires moderate-to-high settlement (Dial and Roughgarden 1998) from a pool of potential recruits (Padisák et al. 1993).

My observations revealed that the above assumptions did not consistently apply to the systems I studied. Assumption (1), i.e. that space is a limiting resource was not met, as communities seldom attained near 100% cover. This was most likely due to environmental background disturbances (discussed below). Assumptions (2) and (3) were alternatively violated in different types of communities. I found three functional community types among the experimental units that were characterized by different mechanisms of coexistence: fast-growing (or re-growing) "turf-communities" and stress-resistant "encrusting-communities" displayed contrary strategies to survive the harsh environmental conditions, while "mixed-communities" incorporated both elements. At one study site (Mabibi) all experimental units were turf-dominated. At the other site (Lala Nek), assemblages consisted mostly of encrusting algae but were transformed to mixed communities with nutrient enrichment.

Mabibi's "turf-communities" were relatively diverse assemblages of low-growing delicate ephemeral algae that typically establish in harsh (e.g. sanded) environments (Hay 1981; Littler et al. 1983; Steneck and Dethier 1994; Cheroske et al. 2000; Sink 2001). Few erect algae were present among the turf, and they were small (less than 2cm) and did not form a canopy. The rapid recovery capacities of turf-forming algae to frequent disturbances rely on their opportunistic re-occupation of freed space associated with their high growth and reproductive rates (Odum 1969; Littler et al. 1983). I observed that experimentally cleared patches were covered with turf within two weeks, which explained the absence of disturbance-induced changes on total biotic cover at Mabibi. Unaltered species richness, evenness and community structure along the gradient of disturbance frequencies indicated that no greater variety of patches of different successional age coexisted in the more frequently disturbed versus the undisturbed treatments, even though the "successional clock" was periodically re-set by my treatment. I infer that "turf-communities" were maintained at early successional stage by the high background disturbances inherent in the system. Hence, the assumption (2) of the IDH, i.e. that succession leads to dominance of the superior competitor was not met in purely opportunistic "turf-communities". My observations correspond with other studies of communities consisting of mostly opportunistic species (e.g. intertidal soft sediments or upland streams) that did not conform to the IDH model of diversity patterns (Lake et al. 1989). They also support the hypothesis that disturbance frequency may have little

effect on diversity in communities that do not have competitive hierarchies (Mackey and Currie 2001).

At Lala Nek's "encrusting-communities", opportunistic colonizers did not establish, possibly due to environmental stress. Thus, assumption (III) of the IDH, i.e. that competitively subordinate species establish opportunistically, was not met and species richness did not respond to the disturbance treatment. Episodic settlement of barnacles did occur in cleared patches, but their effect on species richness and biotic cover was reduced by high post-settlement mortality. The strong temporal variability of barnacle recruitment points out a weakness of the IDH in that it assumes the existence of a pool of potential recruits (Padisák et al. 1993). Particularly for marine organisms with sessile adults and pelagic larvae (such as barnacles), disturbance-independent fluctuations in recruitment can interfere with the mechanisms of the IDH (Dial and Roughgarden 1998).

Only under high nutrient availability at Lala Nek was the coexistence of species regulated according to the mechanisms of the IDH: competitively dominant encrusting algae coexisted with opportunistic turf-forming algae as "mixed-communities". In such relatively diverse assemblages species richness declined with increasing disturbance frequency, while evenness increased. Thus disturbance reduced common and eliminated rare species. The observed diversity pattern represents the descending part of the IDH curve, as expected from the fact that the experimental treatment was superimposed on a substantial background of natural disturbance.

My results show that the applicability of the IDH depends on defined assumptions and mechanisms that are not necessarily met in all natural systems. Yet it is advisable to redefine the IDH as a conceptual framework within certain limits rather than simply rejecting its validity. The practical merits of the IDH have led to its implementation in a multitude of conservation concepts and management plans that have profited from the associated paradigm shift from static to dynamic systems. Hence, its currently wide application should be refined by identifying the factors and mechanisms by which species or assemblages differ in their reaction to disturbance.

Environmental background

Substantial natural disturbances inherent in the intertidal systems studied, such as by sand scouring, desiccation, osmotic effects of precipitation, wave action and extreme tides, formed the background upon which my manipulative disturbance treatment was superimposed. Thus, the experiment lacked true absence of disturbance (control) and probably even lacked low disturbance treatments, and so failed to test the increasing portion of the IDH curve.

Significant heterogeneity amongst blocks of equal treatment reflecting the high natural patchiness associated with wave-exposed (Menge and Branch 2001) and sand-inundated habitats (Daly and Mathieson 1977; McQuaid and Dower 1990; Sink 2001) may have obscured the detection of significant disturbance effects. Sand cover was monitored as possible factor, but failed to

single-handedly explain the observed differences in community structure. Among other unaccounted-for environmental variables, sand scouring is a particularly powerful natural disturbance (Sousa 1979a; Littler and Littler 1981) and determinant of intertidal community structure and diversity (Daly and Mathieson 1977; D'Antonio 1986; Dower 1989; McQuaid and Dower 1990; Sink 2001). Scouring noticeably interfered with the disturbance manipulations by additional clearing of substrate.

Moreover, at the commencement of disturbance and productivity manipulations the communities had not yet fully matured, as evident from low species cover and species richness. Therefore, the treatment was applied on early successional communities, which may have interfered with the effect of disturbance frequency on species structure and diversity.

Effects of productivity

This study experimentally assessed the effects of nutrient enrichment on diversity and community structure, which represents one leg of the supposedly bi-directional productivity-diversity relationship. Nutrient input to coastal nutrient-poor systems has been reported to boost growth rates of primary producers and consequently system productivity (Fujita 1985; Moncreiff et al. 1992). The fact that productivity can also be enhanced by changes in community structure, when slow-growing organisms are replaced by faster-growing ones (Bokn et al. 2003), gives an idea of the complexities that haunt the productivity–diversity relationship. Below, I discuss

productivity as a cause of changes in community structure and diversity and not as an effect, although this may be an over-simplification of the actual complexity of this bi-directional relationship (Waide et al. 1999; Worm and Duffy 2003). Rather than expecting linear or hump-shaped responses to the treatment, a regulation by indirect effects and feed-back loops can give rise to complex non-linear patterns, which might be responsible for the inconsistencies of the productivity-diversity relationship encountered in the literature.

For an assessment of the productivity–diversity relationship it is necessary to distinguish between productivity *per se* (as a function of the organisms) and productivity potential (as a function of the environment) (Worm and Duffy 2003). Fertilizer treatments manipulate the productivity potential, which corresponds to an increase in productivity only if nutrients are a limiting factor for the organisms' growth and reproduction. Coastal waters off the east coast of South Africa, where the study was done, are characterized by low natural nutrient levels and low productivity (Bustamante et al. 1995). Evidence for actual nutrient limitation in my study was given by the observed increase of average community dry mass at both sites with nutrient enrichment. I conclude that the nutrient additions in the experiment effectively increased productivity.

Over and above the substantial background noise, the experiment revealed a significant biological response to nutrient enrichment in both "turf-dominated" and "encrusting-communities". *In situ* nutrient (N and P) and

chlorophyll *a* concentrations failed to provide a quantitative indication that enrichment was accomplished. I assume that due to water turbulences and dilution, the enrichment was simply not detectable in the water column at the instants of sampling. Due to the lack of information about the actual concentrations of nutrient levels, the exact shape of the productivity-diversity relationship could not be deduced from this experiment. This perpetuates a problem common to many studies relating productivity to diversity: where to position a set of communities on the productivity-diversity gradient. Do they fall on an ascending portion of the curve, a descending portion or directly straddle the 'hump'?

The discovery that community structure differed among different nutrient treatments at both sites supports the idea that productivity affects species interactions (Worm et al. 2000). The way communities change with enrichment provides insight in the mechanisms that determine the shape of productivity–diversity relationship. Different mechanisms reigned in "turf-dominated" versus "encrusting-communities".

At Mabibi, nutrient enrichment not only affected individual growth rates but also the re-colonisation of open space by turf-forming algae, as reflected in the greater overall biotic cover at high enrichment. Adapted to high-stress regimes, turf-forming algae seem to most efficiently utilize pulses of nutrients to increase their chance of survival. The green alga *Cladophora coelothrix* in particular thrived with increasing productivity. Species richness was not affected by enhanced productivity, while evenness declined due to the

increased dominance of *C. coelotrix*. Hence my findings at Mabibi do not agree with the prediction that an increase in productivity leads to higher diversity as long as nutrients are a limiting resource (Hall et al. 2000; Worm et al. 2002). Neither could I confirm the general notion that fertilization reduces diversity (Rajaniemi 2003), even though evenness decreased with nutrient additions. The reason I offer for the absence of an effect of productivity on species richness or diversity in turf-communities is that the survival of species was not only limited by resource stress (nutrient limitation) but also by extreme physical conditions. Only few species are adapted to withstand the harshness of a wave-beaten and sand-smothered intertidal system. Thus, enhancing productivity affects the relative abundance but not the species composition in these hardy assembalges. Kondoh's unifying model of productivity, disturbance and diversity (Kondoh 2001) proposes an increase of species richness with raised productivity in extremely disturbed systems (Fig. 4). This pattern is produced through a trade-off between competitive abilities and colonisation rates of species. Based on my observations, I object that evolutionary limits of species survival may override the ecological processes underlying the model.

At Lala Nek, the "encrusting-communities" became transformed with nutrient enrichment into "mixed" communities, where resistant encrusting algae coexisted with barnacles and a variety of turf-forming biota. Enrichment did not seem to have much effect on growth rates of the slow-growing encrusting algae, but rather hindered their spatial dominance by promoting

the establishment and growth of opportunistic turf-forming algae. Consequently, species richness increased with high nutrient availability along with a steady increase in evenness. In contrast to the diversity pattern observed in "turf-communities", "encrusting-communities" behaved according to the predictions of Kondoh (2001) (Fig. 4) that in highly disturbed systems diversity should increase with productivity. Additionally, the observed mechanisms match (a) the *Total Competiton Intensity Theory* (Grime 1977) as well as (b) the *Dynamic Equilibrium Theory* (Huston 1979, 1994). My observations represent the increasing portion of their proposed hump-shaped productivity-diversity pattern (Fig. 2), since (a) nutrient additions led to coexistence of species that are tolerant of stress (encrusting algae) and species that are better competitors for newly available resources (turf-forming algae); and (b) enhanced productivity coincided with an increase of population growth rates, such that growth-limited populations (turf-forming algae) could become established beside populations adapted to resource stress (encrusting algae).

To summarize insights regarding the effects of productivity, my findings show that competition for limiting resources determines algal community structure (Fong et al. 1993; Worm et al. 2000). Because I was unable to quantify the magnitude of my nutrient enrichment, the exact shape of the productivity-diversity relationship could not be deduced from this experiment. Different trends of species richness existed along the nutrient gradient, which corresponded to different functional community types. Thus,

alternative mechanisms affecting species coexistence may act as responses to changing productivity. The claim that diversity increases with nutrient input in oligotrophic marine ecosystems (Hall et al. 2000) was only true when nutrient additions prevented the prevalence of a superior competitor in favour of a number of opportunists (in the encrusting-communities). In this case I found that nutrient enrichment notably increased the growth rate of fast-growing seaweeds, but only marginally influenced the growth of slow-growing seaweeds, as observed in other litteral hard-bottom communities (Bokn et al. 2003). Such interspecific differences contribute to the proposed patterns of the productivity–diversity relationship. However, I agree that the classical view of this relationship incorporates a number of interacting mechanisms of coexistence (Waide et al. 1999). The way forward requires distinction among the underlying mechanisms before generalities about the shape of the productivity-diversity relationship can be proclaimed.

The interactive effects of disturbance and productivity

Regarding the interactive effects of disturbance and productivity on diversity, my results support Huston's (1979) as well as one of Kondoh's (2001) predictions, that in frequently-disturbed systems diversity increases with enhanced productivity. The basis for this phenomenon lies in interspecific differences in the opportunistic utilization of nutrient pulses for growth and reproduction, which results in differences in the regenerative and competitive potentials of species. However, I failed to find a consistent pattern of

interactive effects of disturbance and productivity on diversity as proposed by Kondoh (2001), possibly due to environmental harshness setting the limits on species' survival rather than my superimposed treatment.

Conclusions

In different functional community types, different trends of diversity existed along the gradients of disturbance and productivity. Thus, alternative mechanisms may affect species coexistence. My findings underline the recent criticism that both the IDH and the proposed hump-shaped productivity-diversity relationship are based on a catalogue of assumptions and intermingled mechanisms (Chesson 1994, 2000; Huxham et al. 2000; Sheil and Burslem 2003; Roxburgh et al. 2004; Shea et al. 2004) that are not necessarily attributes of all natural communities. Life history traits of species that directly or indirectly affect species coexistence, such as recruitment, growth, competition and resistance to stress (Sheil and Burslem 2003; Shea et al. 2004) determine how communities respond to disturbance and productivity. Predictive knowledge of factors that affect diversity should therefore be based on mechanisms rather than patterns, with particular focus on the way environmental gradients influence the processes that maintain diversity.

Generalisations of ecological principles need to be based on comparisons that span sufficient temporal and spatial scales. Valuable information regarding the interactive effects of disturbance and productivity on diversity will be provided from replicates of my experiment that were simultaneously

conducted in Australia (Stehbens *et al.* in prep.), Brazil (Klein *et al.* in prep.), Chile (Valdivia *et al.* in prep.) and - starting 6 months later – in Japan, Sweden, Italy, Portugal and Great Britain (M. Wahl & M. Molis pers. comm.).

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